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## A NEW SPECIES OF A GIANT *THOMASOMYS* (MAMMALIA: MURIDAE: SIGMODONTINAE) FROM THE ANDES OF NORTHCENTRAL PERU

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*Abstract.*—We describe *Thomasomys apeco*, new species, from the upper montane forest zone of the eastern slope of the Andes of northcentral Perú (department of San Martín, Río Abiseo National Park). This impressive mammal is the largest known living thomasomyine rodent, exceeded in size of skull and dentition only by the extinct *Megaoryzomys curioi* from the Galápagos Islands, Ecuador.

*Resumen.*—Describimos *Thomasomys apeco*, nueva especie, de la vertiente oriental de los andes al nordeste del Perú (departamento de San Martín, Parque Nacional Río Abiseo). Este llamativo animal es el mas grande de los thomasomios vivientes, siendo superado en tamaño de cráneo y dentición solo por *Megaoryzomys curioi* de las Islas Galápagos, Ecuador.

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In 1987, the Peruvian Association for the Conservation of Nature (APECO), with the financial assistance of the David and Lucile Packard Foundation, began a four-year faunal survey and inventory of the Río Abiseo National Park located in western departamento San Martín, Perú (Fig. 1). The park, centered at approximately 07°45'S, 77°15'W, covers 2745 square kilometers encompassing the major part of the Río Abiseo watershed on the eastern (Amazonian) slope of the Andes and drains into the Río Huallaga. The elevational range is from near 1000 to more than 4000 m and includes seven identified life zones according to the Holdridge Life Zone classification (Tosi 1960) as modified by Young & León (1988). Surveys during the first year of study were at higher elevations (from about 3000 to 3600 m) in Tropical Alpine Zone and Tropical Montane Rain Forest (Paramo Pluvial Alpino and Bosque Pluvial Montano Tropical, respectively; Tosi 1960). These wet paramo and elfin forest habitats produced a variety of small mammals including a previously undescribed giant thomasomyine rodent that may be known as:

### *Thomasomys apeco*, new species

*Holotype.*—Adult male, Museo de Historia Natural of the Universidad Nacional Mayor de San Marcos (MUSM) 7197, from Valle de Los Chochos, ca. 25 km NE Pataz, 3280 m, Parque Nacional Río Abiseo, San Martín, Perú. Collected by Mariella Leo L. on 27 Jul 1987, original number MLL 055. The holotype is a well-made skin with skull and mandibles (latter separated at symphysis) in good condition, except that tip of right paroccipital process is missing (broken).

*Paratypes.*—Eight paratypes (skins with skulls and mandibles): MUSM 7199 female from the type locality; MUSM 7196 female (with body in fluid), MUSM 7203 female, MUSM 7204 female, MUSM 7202 female, MUSM 7201 male, and MUSM 7198 female from Pampa del Cuy, ca. 24 km NE of Pataz, 3260–3380 m; and MUSM 7200 male from Puerta del Monte, ca. 26 km (at 60°) from Pataz, 3250 m.

*Distribution.*—Known only from the vicinity of the type locality and the neighboring Pampa del Cuy Valley to the south.

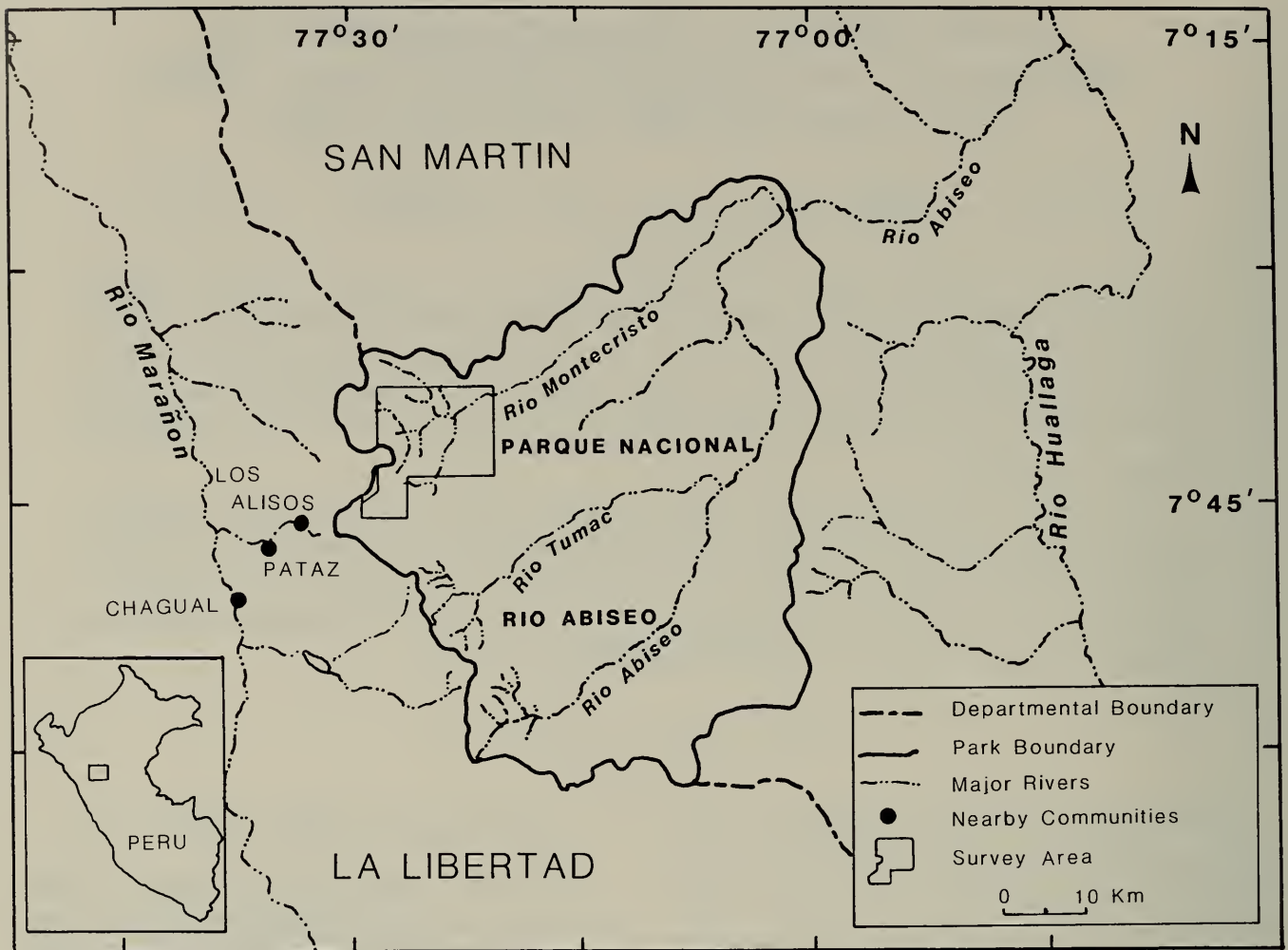


Fig. 1. Map of Río Abiseo National Park showing location of area where inventories were conducted. The western boundary of park corresponds to border between departments of La Libertad and San Martín.

Puerta del Monte is in the lower Pampa del Cuy Valley.

*Etymology.*—The name is based on the acronym APECO (Asociación Peruana para la Conservación de la Naturaleza), the Peruvian Association for the Conservation of Nature responsible for conducting the faunal inventory of the Río Abiseo National Park. The species epithet *apeco* is treated as a noun in apposition. The singular genitive endings *-i* or *-ae* are not appropriate because these endings are for modern personal names.

*Diagnosis.*—*Thomasomys apeco*, endemic to the northeastern Andes of Perú, is the largest living thomasomyine and, along with *Kunsia tomentosus* (Lichtenstein, 1830), *Nectomys squamipes* (Brants, 1827), and the extinct *Megaoryzomys curioi* (Niethammer,

1964) and *Megalomys* spp., is among the largest Sigmodontinae known (Gyldenstolpe 1932, Steadman & Ray 1982, Nowak 1991). The combination of large size, long black and white tail, and long unwebbed hind feet distinguish this species from other sympatric Sigmodontinae and related thomasomyines. Dental features that distinguish this species from other large *Thomasomys* include the especially well-developed anteroloph and parastyle on M1 (dental terminology follows Reig 1977; also see Carleton & Musser 1989), connection of anteroloph to anterior mure independent of anterolabial conule and its connecting loph, well-developed posteroloph of M1 and M2 whose labial extension (beyond metaloph) persists in well-worn teeth, decidedly anterior-posterior orientation of metalophids

Table 1.—Measurements of *Thomasomys apeco* new species, from Parque Nacional Río Abiseo, San Martín, Perú. Linear measurements are in millimeters and mass in grams; values are the mean followed by range in parentheses. Age-class categories defined in text.

Measurement	Age 1 ( <i>n</i> = 1, ♂)	Age 2 ( <i>n</i> = 6, 4 ♀ + 2 ♂)	Age 3 ( <i>n</i> = 1, ♀)	Age 4 ( <i>n</i> = 1, ♀)
<b>Length</b>				
Total	469	504.3 (469–548)	560	558
Tail	299	303.3 (279–329)	324	320
Hind foot (cu)	56	53.8 (50–59)	54	55
Ear (from notch)	31	28.7 (27–31)	31	31
Skull	45.2	48.1 (44.3–50.9)	50.5	51.0
Condylbasal	42.6	45.1 (41.9–47.7)	47.7	47.8
Nasal	16.3	17.8 (16.3–19.1)	18.9	18.7
Palatilar	20.1		22.3	22.6
Post palatal	15.5		18.3	18.7
Incisive foramina	9.6	10.6 (9.4–11.7)	11.3	11.4
Maxillary tooththrow (alveolar)	10.1	9.8 (9.4–10.1)	10.2	10.0
<b>Breadth</b>				
Zygomatic	24.8	25.5 (23.6–27.4)	27.0	27.1
Mastoidal	broken	17.8 (17.2–18.2)	18.6	18.2
Postorbital	5.3	5.2 (4.9–5.4)	5.0	5.2
Palatal (postdental constriction)	7.9		7.6	6.9
Rostral	8.8	8.7 (7.8–9.8)	9.9	9.7
Mass	190	223.3 (164–335)	258	300

and entolophids (and correspondingly long meso- and posteroflexids) in the first two lower molars (a feature shared with *T. aureus* [Tomes, 1860]), crescent-shaped posterolophid on m1 extending to lingual margin of tooth, and m3 similar in form to m2 because of large, well-developed entoconid. Also distinctive is the thick, well-developed jugal and the relatively deep notch between

the lacrimal and the zygomatic ramus of the maxilla.

*Measurements of the holotype.*—Linear measurements are in millimeters and mass (weight), in grams: Total length, 498.0; tail, 300.0; hind foot, 50.0; ear, 27.0; greatest length of skull, 50.2; condyloincisive length, 45.9; palatilar length, 22.4; postpalatal length, 17.8; incisive foramen length, 11.7;



Table 2.—Measurements of *Thomasomys apeco* new species, *Thomasomys aureus* complex, and *Megaoryzomys curioi*. Age classes of *T. apeco* and *T. aureus* complex are combined. Measurements of *Megaoryzomys curioi* from Steadman & Ray (1982:6). Linear measurements are in millimeters and mass in grams; values are the mean followed by range (in parentheses) and sample size. See "Additional Specimens Examined" for sources of *T. aureus*.

Measurements	<i>T. "aureus"</i>	<i>T. apeco</i>	<i>M. curioi</i>
Length			
Total	372.4 (335–421) 10	514.3 (469–560) 9	
Tail	218.6 (199–248) 10	307.0 (279–329) 9	
Hind foot (cu)	36.7 (33–41) 10	54.0 (50–59) 9	
Ear (from notch)	23.2 (21–24) 10	29.4 (27–31) 9	
Skull	38.2 (34.6–41.8) 12	48.3 (44.3–51.0) 9	55.6
Condylobasal	35.9 (31.9–40.1) 13	45.4 (41.9–47.8) 9	54.5 (53.3–55.6) 2
Condylolincisive	33.9 (30.7–38.6) 13		
Palatilar	16.0 (13.9–18.4) 13		25.3 (24.6–26.5) 3
Postpalatal	14.0 (12.5–16.5) 13		
Incisive foramina	8.1 (7.1–9.1) 13	10.6 (9.4–11.7) 9	10.8 (9.6–11.7) 5
Nasal	14.4 (12.4–15.8) 12	17.9 (16.3–19.1) 9	
Rostrum	14.2 (12.4–16.0) 12		
Maxillary tooththrow	7.3 (6.8–7.8) 13		10.9 (10.0–11.5) 5
Maxillary tooththrow (alveolar)	7.5 (7.0–8.1) 13	9.9 (9.4–10.2) 9	11.5 (10.9–12.3) 13
Mandibular tooththrow	7.5 (6.8–8.0) 13		12.1 (11.5–12.7) 9
Breadth			
Zygomatic	20.1 (18.6–21.4) 13	25.8 (23.6–27.4) 9	34.3 (33.8–34.8) 2
Braincase	14.8 (13.9–15.5) 13		19.0 (18.7–19.2) 3
Mastoidal	14.8 (13.9–15.9) 12	17.9 (17.2–18.6) 8	
Postorbital	4.9 (4.3–5.3) 13	5.2 (4.9–5.4) 9	8.2 (7.3–8.6) 4
across molars (M2–M2)	7.7 (7.3–8.5) 13		
Palate (postdental constriction)	6.0 (5.4–6.8) 13		
Rostral	6.8 (6.1–7.2) 13	8.9 (7.8–9.9) 9	11.7 (11.0–12.3) 3
Zygomatic plate	3.1 (2.5–3.7) 13		8.1 (6.9–8.7) 6

Table 2.—Continued.

Measurements	<i>T. "aureus"</i>	<i>T. apeco</i>	<i>M. curioi</i>
Depth			
Braincase	11.2 (10.2–11.9) 13		
Mass	91.8 (58–136) 9	232.0 (164–335) 9	

nasal length, 19.4; zygomatic breadth, 25.7; braincase breadth (above zygoma), 25.7; mastoidal breadth, 18.1; interorbital constriction, 5.4; breadth across molars (M2-M2), 9.9; palatal breadth (post dental), 7.1; rostral breadth, 8.8; rostral length, 19.3; zygomatic plate breadth, 4.3; mesopterygoid fossa breadth, 3.5; maxillary tooth row length, 9.5; alveolar maxillary tooth row length, 9.7; mandibular tooth row length, 9.9; alveolar mandibular tooth row length, 9.5; mandibular length; 28.2; mass, 249.0.

*Additional measurements.*—See Tables 1 and 2 for additional measurements.

*Description.*—Dorsal fur long (under fur as long as 22 mm middorsally with guard hairs reaching 30 mm) and broadly dark gray based (between Slate-Gray and Slate Color; capitalized color terms from Ridgway 1912), slightly darker subterminally, and broadly tipped with paler. Guard hairs black, conspicuous, and imparting a coarse quality to the fur. Dorsum bright with color varying between individuals from Raw Sienna to Ochraceous-Tawny and Tawny Olive streaked with black (guard hairs). Color darkest middorsally and becoming gradually clearer (less streaked with black) over shoulders, sides, and flanks where color grades into Cinnamon or Cinnamon-Buff, becoming Ochraceous-Buff on venter. One age-class-1 male (MUSM 7200) with shorter and harsher pelage from nape to middle of back that may be remnant of juvenile pelage; otherwise colored as in adults. Ventral coloration brightest along sides where it may encroach toward ventral midline, and

on band across chest and along thoracic midline. Extent of Ochraceous-Buff coloration on venter variable among individuals, most extensive on MUSM 7199 where nearly entire ventral surface is uniformly colored; somewhat less extensive on MUSM 7200 where coloration is strongest on chest (both as a pectoral band and along thoracic midline); and least extensive on MUSM 7196 where coloration is brightest only on middle of chest (thoracic midline) and in perianal region. The main color differences between specimens seem related to the extent of yellow pigment in hair tips. The narrower the terminal color band, the paler the color (approaches Pale Buff) and the more conspicuous the basal gray color of the fur. Fur on throat dark gray based, tipped with buff to whitish, and usually paler than remainder of venter. Fur on chin (below lower incisors) white to base. Eye ring somewhat darker than remainder of head, which otherwise is colored like the dorsum. Ears clothed inside and out with short dark brown to blackish hair and lack evidence of a pale rim. Although fur behind and below ears clearer (less black-lined) than remainder of head, post or subauricular spots characteristic of many thomasomyines absent. Ankles completely encircled with blackish hair (near Fuscous Black), with the same color extending over outer upper surface of hind feet and base of toes to claws. Claws, digital bristles, and inner (and sometimes outer) dorsal surface of metatarsals conspicuously paler than remainder of hind foot. Outer edge of wrist and metacarpals whitish with



a few long white tactile hairs; otherwise, forefeet dark with paler claws and digital bristles. Tail longer than head and body (57 to 60% of total length) and weakly penicillate. Color on basal two-thirds to three-fifths of tail dark brown to blackish with terminal one-third to two-fifths white. Vibrissae long (some exceeding 70 mm), a few either uniformly pale or dark brown throughout, but most dark brown with pale tips. Hind feet long; plantar surface naked to ankle. Hallux shortest with base of claw well short of first phalanx on digit II. Middle three toes of hind foot nearly of equal length with digit III only slightly longer than digits II and IV; tip of claw of digit V extends to base of claw of digit IV.

Skull large and robust with flaring zygomatic arches and narrow postorbital constriction (Fig. 2). Nasals long, subparallel above rostral capsules, and terminate at nearly same level as posterior extensions of premaxillae. Margins of postorbital constriction elevated (but not beaded) and define the pronounced depression (groove) on frontals along midline of skull. Dorsal profile low and sloping forward along nasals over rostrum. Squamosal roots of zygoma massive and flaring with posterolateral ridge converging toward lambdoidal crests in a nearly straight line giving braincase a V-shaped lateral profile when viewed from above. Auditory bullae relatively large, although not extending below plane of pterygoid processes. Mastoid not fenestrate. Parapterygoid fossae equal to or narrower than mesopterygoid fossa. Alisphenoid strut present, although its development variable (missing on one side in one individual). Sphenofrontal foramen and associated squamosal-alisphenoid groove (see Carleton & Musser 1989:fig. 20) on lateral floor of braincase absent.

Upper incisors orthodont; upper and lower incisors normal for genus. Upper molars robust, always longer (anteriorly-posteriorly) than wide, and forming a graded series

(Fig. 3). First upper molar with well-developed, comparatively broad anteriomedial flexus, which opens anteriorly onto a shallow basin rimmed anteriorly by a low ridge bearing a variable number of accessory cusps and lophules (dental terminology follows Reig 1977). Protoloph short and weakly developed or absent. Anteroloph and anterostyle well developed with the latter expanded anteriorly-posteriorly at margin of tooth. Anteroloph, anterior mure, and loph connecting anterolingual and anterolabial conules to anterior mure appear to arise from a common juncture in unworn teeth (anteromedian flexus, anteroflexus, protoflexus, and anteromedial bend of paraflexus converging), although anterolingual loph becomes more isolated in worn dentition. Posterior end of anteromedial flexus (anterior internal fold of Hershkovitz 1944) isolated as a small, shallow enamel island in some individuals. Anteroloph well developed and continuous from anterior mure to labial margin in M2 and M3. A low anterior cingulum forms anterior margin of protoflexus in M2 and M3. Paraloph in all three upper molars joins median mure between junctures of protoloph and mesoloph. A paralophule also extending from paracone to mesoloph (connection may be incomplete in M3), resulting in isolation of median portion of mesoflexus as an enamel island. Well-developed mesoloph extending to labial margin in all three molars. Metaloph joining posteroloph at approximately mid-length in M1 and M2 in unworn dentition (connection appears closer to labial margin in worn teeth because of attrition of posteroloph). The broad hypoflexus may contain low accessory cusps on lingual margin. Enteroloph either absent or, at best, visible in unworn teeth only as a lateral swelling from the median mure in M1 and M2. The small metacone on M3, although visible in unworn teeth, becoming more difficult to locate as tooth wears.

Lower molars also form a graded series;



Fig. 2. Dorsal, ventral, and lateral views of cranium, and lateral view of mandible of holotype of *Thomasomys apeco*, new species, MUSM 7197 (original number MLL 055). Vertical bar equals 10 mm.



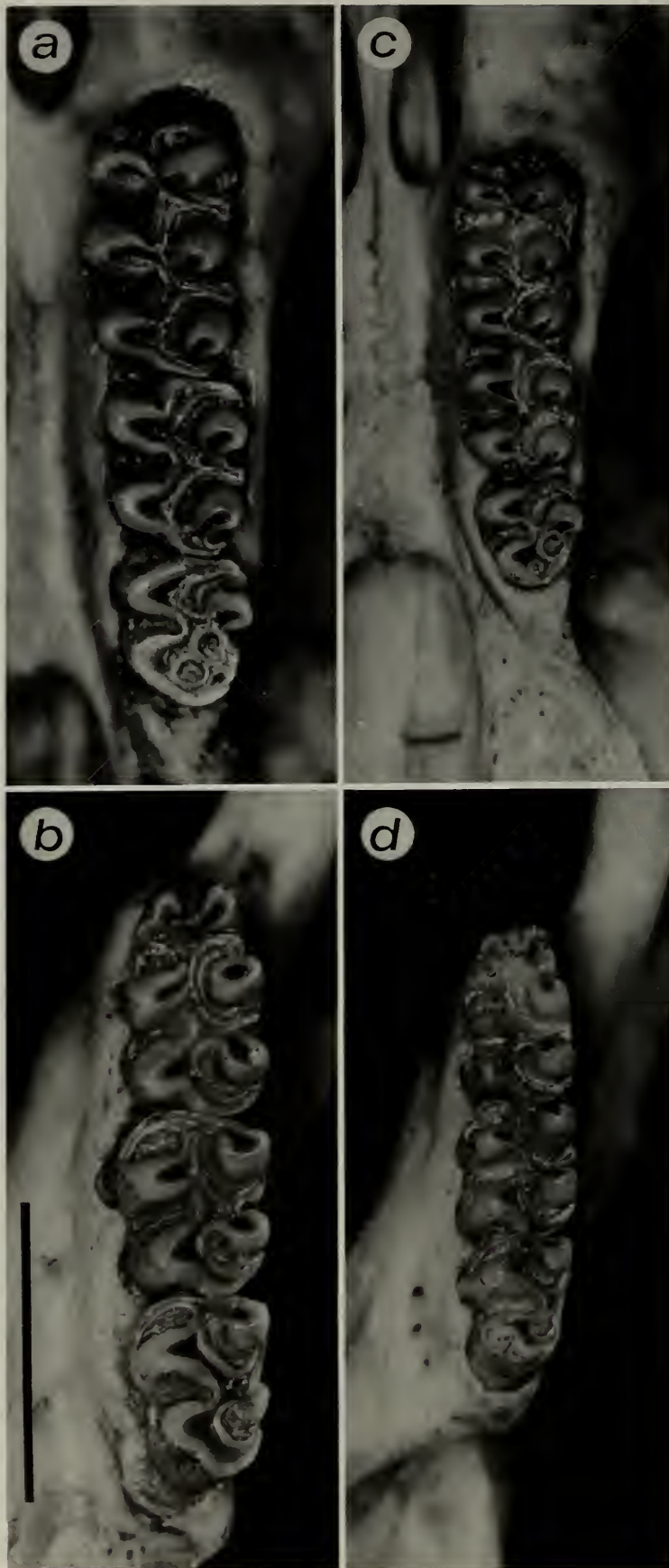


Fig. 3. Left maxillary and mandibular tooththrows of *Thomasomys apeco*, new species, and *T. aureus* (Tomes, 1860): *T. apeco*, MUSM 7198, *a* maxillary and *b* mandibular; *T. aureus*, MLL 312, *c* maxillary and *d* mandibular. Vertical bar equals 5 mm.



however, m3 is similar to m2 in length and development of the entoconid, although narrower posteriorly. The prominent and deep anteromedial flexid separates high, but relatively narrow, lingual and labial conulids (each about one-half size of metaconid). The short and weakly-developed protolophid inconspicuous; in its place, the anterolabial margin of m1 enclosed by a prominent anterolabial cingulum extending posteriorly from outer surface of anterolabial conulid to protoconid base. Anterolabial cingulum in m2 and m3 fused to protoconid and, with moderate tooth wear, enclosing protoflexid as a comma-shaped island. Metalophid continuous with lateral extension of anterolophid in all three lower molars, reflected by long mesoflexid separating metacone and median mure. The narrow anteroflexid extends to anterior mure (evident in all but well-worn teeth). The shallow metaflexid partly confluent with anteroflexid. Mesostylid fused to posterolateral margin of metaconid in each molar and, with relatively little wear, connection isolates mesoflexid as internal island. Protolophid narrower than protoconid and directed slightly anteriorly as it joins median mure. In m1, both entolophid and entolophulid join mesolophid, reflected by long posteroflexid separating entoconid from median mure. In m2 and m3, entolophid joins median mure at level of anteriormost connection of hypolophid and median mure. Entolophulid extending to mesolophid resulting in short, narrow entoflexid whose medial extension becomes a small enamel island lost relatively early in wear, at which time entolophid assumes a quite broad appearance. Entolophulid of m1, evident only in unworn teeth, isolating medial entoflexid as small enamel island (internal entoflexid) lost early in wear, at which time evidence of entolophulid is lost. Despite original double connection, resultant entolophid narrower than entoconid. The relatively broad hypoflexid extending to near midline in m1

and m2, and approximately two-thirds width of tooth in m3. In all three lower molars, hypoflexid may contain one or more small cusplids at outer margin. A shallow flexid indents posterolabial side of each molar at juncture of posterolophid and hypolophid. Distal end of posterolophid in m1 and m2 lies close to entoconid and, with relatively little wear, appears fused to entoconid isolating posteroflexid as an island. In m3, posteroflexid appears enclosed only in well-worn teeth. Lower molars with decidedly anterior orientation of metalophids and entolophids (and correspondingly long meso- and posteroflexids) in m1 and m2 along with the relatively well-developed entoconid in m3 and correspondingly shallow hypoflexid.

Age categories based on teeth wear are defined as follows: Age 0, all cheek teeth not fully erupted and functional; age 1, all teeth erupted and functional, lingual cusps showing relatively little wear; age 2, lingual cusps worn, but not flat, occlusal surfaces showing some wear on all cusps; age 3, all lingual cusps on M2 and M3 worn flat, labial cusps showing wear; age 4, all cusps worn, occlusal surface of M3 flat, some major dental features may be obliterated.

*Comparisons.*—Among known species, *T. apeco* needs comparison with only *Megaoryzomys curioi* and the species of large *Thomasomys* comprising the *T. aureus* complex. *Megaoryzomys curioi* is larger (see Table 2) with relatively square molars and a shallow notch between lacrimal and zygomatic ramus of maxilla (see Steadman & Ray 1982:figs. 7D and 9A-lower). Dental characteristics (e.g., paraloph joins paracone to median mure; compare A and B in Steadman & Ray 1982:fig. 4) place *M. curioi* well apart from other known species of larger thomasomyines. Although *T. apeco* approaches *M. curioi* in size, dental features suggest closer affinity with species of the *T. aureus* complex. The only major dental differences we have found that separate *T. ape-*

*co* from specimens of *T. aureus* from Perú, including Río Abiseo National Park, are the more medial orientation of the paroloph in M1 and M2, more prominent anterior mure in M2, relatively larger and more widely separated anterior conulids in m1, more rounded posteroloph in m1 and m2, and larger entoconid on m3 with a correspondingly shorter hypoflexid that result in similar appearance of m2 and m3 (Fig. 3). Cranial features other than larger size (Table 2) that can be used to distinguish *T. apeco* from *T. aureus* are the shallower zygomatic notch, much deeper notch between lacrimal and zygomatic ramus of maxilla, and much thicker jugal. The larger and thicker jugal in *T. apeco* results in a greater distance between distal ends of maxillary and squamosal contribution to the zygomatic arch (distance exceeds greatest depth of zygomatic arch at its midpoint). The jugal is conspicuously thin in *T. aureus* and the gap between ends of maxilla and squamosal filled by the jugal is less than the greatest depth of the zygomatic arch at its midpoint. Externally, *T. apeco* is much larger and more robust than *T. aureus* and, although proportionally about the same length (from 56 to 61% of total length), the tail is white distally for nearly half its length in contrast to being uniformly dark in *T. aureus*.

*Additional specimens examined.*—Specimens we examined are deposited either in the collections of the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Perú (MUSM); the National Museum of Natural History, Washington, D.C., U.S.A. (USNM) [division of mammals,], USNM-P [paleobiology]); or are indicated by field numbers (MLL [Mariella Leo L.] and MRR [Mónica Romo R.]). The majority of the latter will be deposited in the MUSM, which commonly has been referred to in the literature as the Museo de Historia Natural “Javier Prado.”

*Thomasomys aureus* complex: Colombia: Cundinamarca, Bogotá, USNM 251957,

topotype of *Thomasomys princeps* (Thomas, 1900); Cundinamarca, Choachí, USNM 251956; Cundinamarca, Laguna Vergón [= Laguna del Verjón], USNM 251976. ECUADOR: Pichincha, Río Condor Huachana, 3.45 km NE of Lloa, USNM 513588, 513589. PERU: San Martín, Río Montecristo, ca. 28 km NE of Pataz, MLL 312; San Martín, Puerta del Monte, ca. 26 km (at 60°) from Pataz, MLL 249; San Martín, Las Palmas, ca. 32 km NE of Pataz, MRR 579 and 594, MLL 340 and 343; San Martín, Las Papayas, ca. 32 km NE of Pataz, MLL 390; Junín, Río Palca, 15 km W of San Ramón, USNM 507265 and 507266; Cuzco, Torontoy, 3260 m, USNM 194818; Cuzco, Tocopoque [= Tocopogueyu], Ocobamba Valley, 3000 m, USNM 194826–194828. *Megaoryzomys curioi* (Niethammer, 1964). ECUADOR: Islas Galápagos, Isla Santa Cruz, USNM-P 284204 (15 molars), USNM-P 284213 (mandible with m2 and m3), 284276 (right M1), USNM-P 284283 (right mandible); USNM-P 284287 (right m1), USNM-P 284343 (right mandible with all molars), USNM-P 284346 (right mandible with m1).

*Remarks.*—One female was pregnant in August 1987 with a single embryo (CR = 5.0 mm); the only female caught the following July showed well-developed mammae. Age-class-2 males had well-developed testes in July and August (length = 23.0 mm), while the age-class-1 male had small testes in July (4.6 mm).

A total of ten specimens were caught of which one was released. The holotype and the age-class-1 female collected at Los Chochos were caught in live traps, one at the end of a log and the other on a bank above a small stream, on the forest floor in an isolated patch of elfin forest. The age-class-4 female was caught at Pampa del Cuy in an unbaited conibear trap set in a runway leading up from a rivulet of water through grass on a slope in wet pampa habitat over a hundred meters from forest. Three were taken



in unbaited live traps placed in a small shallow stream bordered by a few small trees in otherwise pampas habitat. Traps (three "Tomahawk") were placed to intercept any animals moving along the stream. The Puerto del Monte specimen was captured within continuous forest. Three additional specimens were trapped in pampas habitat associated with a small stream bordered by bushes and scattered small trees. One of these was dusted with fluorescent powder and released. Subsequent trailing of this animal showed that it had climbed a small tree and followed a branch to a bank above the stream where originally caught.

Stomach morphology of MUSM 7196 (age-class-4 female) shows similarity to that described and illustrated by Carleton (1973: 14) for a *T. aureus* from Perú in contrast to the morphology he described for other species of *Thomasomys*. The stomach of our *T. apeco* was not sufficiently distended to permit a detailed comparison; nevertheless, while extension of cornified epithelium into the antrum is extensive, it is not as extreme as in *T. aureus* and does not separate the glandular epithelium into two zones.

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